

ACCLIMATION OF OXYGEN CONSUMPTION TO TEMPERATURE IN THE AMERICAN COCKROACH (*PERIPLANETA AMERICANA*)¹

PAUL A. DEHNEL² AND EARL SEGAL³

Department of Zoology, University of California, Los Angeles, 24, California

The extensive literature that shows metabolic compensation to temperature among marine poikilotherms (see Dehnelt, 1955; Segal, 1955; for reviews) has led us to question the generally reported inability to compensate among insects. Scholander, Flagg, Walters and Irving (1953), having compared certain arctic and tropical insects, find no significant metabolic adaptation to temperature. Edwards (1953) generalizes: he proposes that the metabolic response of insects to temperature can be expressed by a single metabolism/temperature curve. Although several examples of insect acclimation are cited by Bullock (1955) he states (p. 320) that "in spite of these cases, it is believed that insects may be relatively poor in ability to compensate."

Of the well documented cases of insect acclimation to temperature, four are either overwintering or in summer sleep (Lühmann and Drees, 1952; Marzusch, 1952); one is aquatic (Sayle, 1928), and one is in pupa (Heller, 1930). Only a single example concerns an active isolated insect (Parhon, 1909).⁴

We have investigated the American cockroach, *Periplaneta americana*, an insect that is active all year, to see whether or not it behaves similarly to marine poikilotherms with respect to temperature adaptation of the oxygen consumption.

MATERIAL AND METHODS

A culture of nymphal and adult cockroaches was obtained from the Riverside campus of the University of California. This culture had been maintained at 27° C. for a minimum of three generations. Neither molting individuals nor adult females nor individuals under approximately 0.3 gram were used in these experiments. The animals were divided into two groups, nymphs and adults, the former being represented by a wide range of instars. Each of the above two groups was subdivided into three groups of randomly selected individuals. There were fifty animals in each of the six groups. One group of nymphs and one group of adults were placed at 10° C. Similar groups of nymphs and adults were placed at 16°

¹ This study was conducted at the University of California, Los Angeles. We wish to thank Dr. T. H. Bullock for making the equipment and space available to us.

² Present address: Department of Zoology, University of British Columbia, Vancouver 8, Canada.

³ Present address: Department of Biology, Kansas State Teachers College, Emporia, Kansas.

⁴ Parker (1930) shows acclimation of growth to temperature in two species of insects (*Melanoplus mexicanus* and *Camnula pellucida*). Thompson (1937) finds that embryos of *Melanoplus differentialis* and *Melanoplus femur-rubrum* kept at lower temperatures (20° C.) show a more rapid heart rate than embryos incubated at higher temperatures (30° and 35° C.) when measured at a series of temperatures from 20° to 35° C.

and 26° C. Cockroaches placed at the latter temperature were at essentially the same temperature as the original stock (26°–27° C.); this permitted them to be used as controls.

In order to eliminate the reported light-controlled diurnal activity rhythm (Cloudsley-Thompson, 1953), the animals were maintained in constant darkness. The cockroaches were weighed after each experiment was completed, as it was felt that the added handling of weighing would stimulate the animals to increased activity.

Each of the six groups of animals was given an initial supply of food, and fresh water was added every other day. It was noticed that the cockroaches at 10° C. did not feed. In order to determine whether non-feeding had any effect on the results, a fresh culture was obtained and the experiment was repeated; this time none of the animals was given food.

Oxygen consumption was measured with the use of Wennesland-Scholander microrespirometers which were submerged in a constant temperature bath controlled to $\pm 0.5^\circ$ C. The cockroaches were kept at the acclimation (10° and 16° C.) and control (26° C.) temperatures for three weeks. At the end of each week measurements were made on a nymphal sample from each of the three temperature groups. At the end of the first and third weeks similar measurements were made on adult samples from each of the three temperature groups. All the above oxygen consumption measurements were made at 20° C. Those cockroaches from 16° and 26° C. were kept in the 20° C. bath for one hour before measurements were made. Animals from 10° C. were kept at 15° C. for one hour; the temperature of the bath was then raised to 20° C. After one hour at the latter temperature, their oxygen consumption was measured.

In addition to the above experiments, two samples of nymphs were separated from the original culture (26° C.). The oxygen consumption of those from the first sample was measured over a descending series of temperatures (30°, 25°, 20°, 15° and 10° C.). The first sample was then placed at 26° C. and the other at 10° C. At the end of three weeks the oxygen consumption of animals from the first sample was measured over the same descending series of temperatures. The oxygen consumption of animals from the second sample was measured over an ascending series of temperatures (10°, 15°, 20°, 25° and 30° C.).

Measurements for all experiments were made at fifteen-minute intervals for a period of one and one-half to three hours. On all figures each point represents one animal. The coordinates are log-log and the curves are eye-fitted.

RESULTS

Nymphs. When the oxygen consumption of equal weight animals kept at 10°, 16° and 26° C. is measured at 20° C., it is found that those animals maintained at the lower temperatures show the higher consumption (Fig. 1). The increase in oxygen consumption of animals kept at 10° and at 16° C. occurs within the first week. For the duration of the experiment no further increases were observed. Under the conditions of this experiment it is impossible to compare the time required for acclimation in the two groups; it can be said only that in both it is complete within one week. Because there is no difference in the weekly oxygen consumption values for each group, they are combined for the regression curves in Figure 1.

For purposes of comparison within the three groups of cockroaches, animals with an average weight of 0.6 gram were chosen from the regression curves. This weight was chosen because it falls approximately within the center of the weight range on each of the regression curves. When the oxygen consumption of this 0.6-gram animal is read directly from the graph it is noted that (1) this weight animal acclimated to 10° C. consumes 67 mm.³/gm./hr. (57%) more oxygen than his counterpart acclimated to 26° C., (2) this weight animal acclimated to 16° C. consumes 42 mm.³/gm./hr. (36%) more oxygen than his counterpart from 26° C. and (3) this weight animal from 10° C. consumes 25 mm.³/gm./hr. (16%) more oxygen than his counterpart from 16° C. It is apparent that the animals acclimated

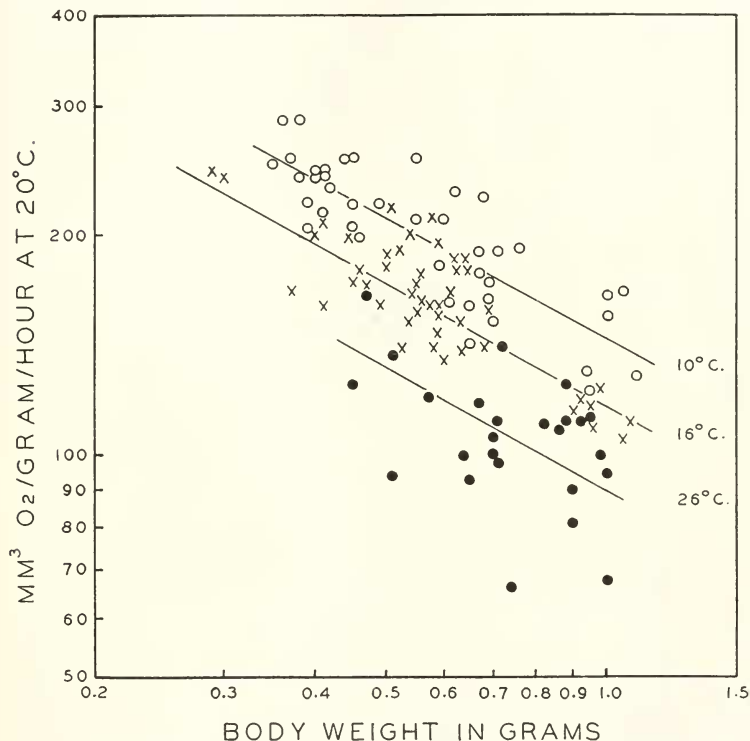


FIGURE 1. Weight-specific oxygen consumption as a function of weight in nymphal *Periplaneta americana*. Animals were kept at 10°, 16° and 26° C. for one to three weeks, and the measurements were made at 20° C. In all figures each point represents the average oxygen consumption for one animal over a period of one and one-half to three hours. Open circles represent 10° C. animals, crosses, 16° C. animals and closed circles, 26° C. ones. The coordinates are logarithmic, and all curves are eye fitted. Results from feeding and non-feeding experiments are combined.

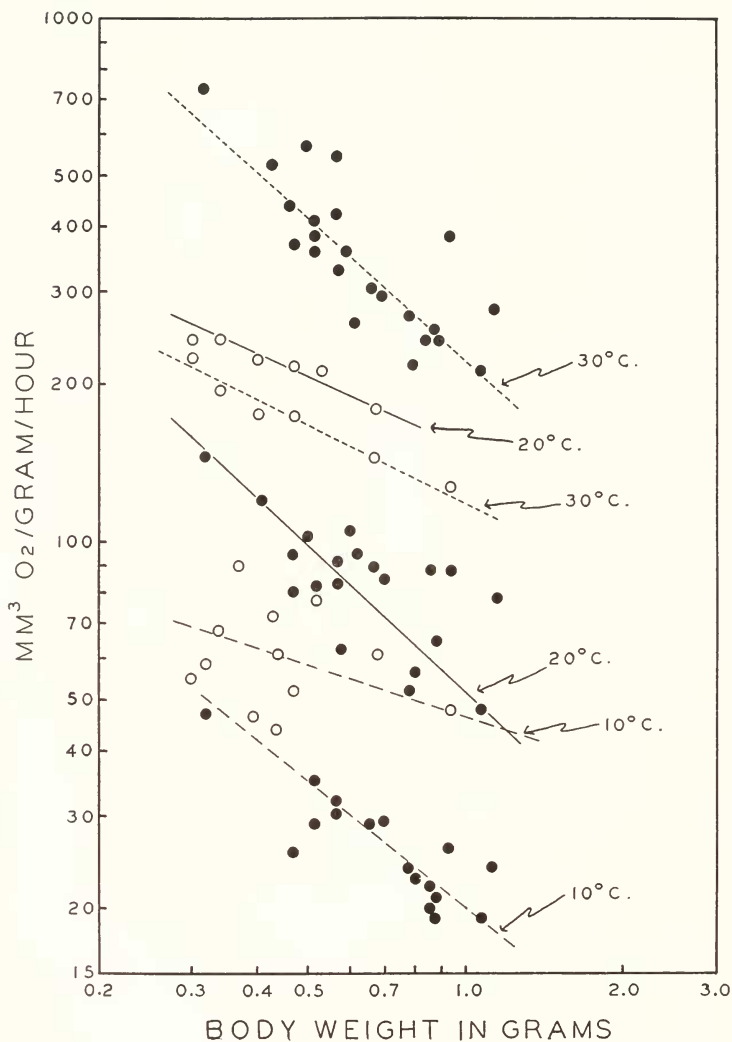


FIGURE 2. Weight-specific oxygen consumption as a function of weight in nymphal *Periplaneta americana* measured over a series of temperatures. Open circles represent cold-adapted animals (10° C.); closed circles represent warm-adapted animals (26° C.).

to 10° C. are responding to the increased distance (° C.) from the control temperature (26° C.) with a further increase in oxygen consumption. The values indicate that a linear relation exists between the increase in oxygen consumption and the decrease in acclimation temperature (4.2 mm.³ O₂/gm./hr. increase per degree centigrade drop in temperature).

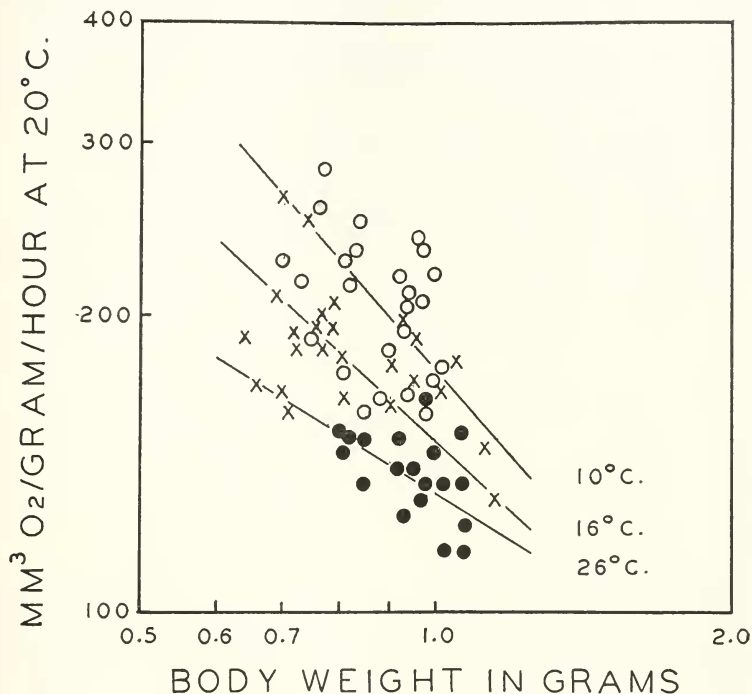


FIGURE 3. Weight-specific oxygen consumption as a function of weight in adult *Periplaneta americana*. Animals were kept at 10°, 16° and 26° C. for one to three weeks, and the measurements were made at 20° C.

Nymphs, rate/temperature experiment. The results of the rate/temperature experiment are presented in Figure 2. The rate values obtained at 15° and 25° C. are omitted to make the graph easier to read. From 10° to 25° C. cold-acclimated nymphs (10° C.) consume more oxygen per gram per hour than equal weight warm-acclimated nymphs (26° C.). The oxygen consumption of the cold-acclimated nymphs is depressed at 30° C., i.e., less oxygen is consumed at 30° C. than at 20° C. Since the curves at 30° and at 20° C. are parallel, the oxygen consumption of large and small nymphs is depressed equally.

At all temperatures the regression lines for the warm-acclimated nymphs are

steeper; the regression lines at the different temperatures for either the warm- or cold-acclimated animals are essentially parallel.

If the curves (Figs. 1 and 2) representing nymphs acclimated to 10° C. and measured at 20° C. are compared, it is seen that the slopes and positions of the curves are the same. However, if a similar comparison is made for the warm-acclimated nymphs, it is found that the oxygen consumption is constantly lower for these animals in the rate/temperature experiment. These animals spent approximately four hours at 30° C., before they were measured at 20° C. It is possible that four hours is sufficient time for the acclimation process to have begun. Therefore, the oxygen consumption at 20° C. is lower than it is for the animals brought directly from 26° to 20° C.

Adults. Adult cockroaches, like nymphal cockroaches, show acclimation of their oxygen consumption to temperature. Those adults kept at 10° and 16° C. consume more oxygen per gram than do equal weight adults kept at 26° C. when all are measured at 20° C. (Fig. 3). As with the nymphs no change was found in the weekly (first and third) oxygen consumption values for each temperature group. Therefore, these values are combined for each of the regression curves in Figure 3.

For the adult cockroaches, animals with an average weight of 0.9 gram were chosen. When the oxygen consumption of this 0.9-gram adult is read from the graph it is noted that (1) this weight animal acclimated to 10° C. consumes 55 mm.³/gm./hr. (40%) more oxygen than his counterpart acclimated to 26° C., (2) this weight animal acclimated to 16° C. consumes 25 mm.³/gm./hr. (18%) more oxygen than his counterpart from 26° C. and (3) this weight animal from 10° C. consumes 30 mm.³/gm./hr. (18%) more oxygen than his counterpart from 16° C. These values suggest that in contrast to the nymphs, a non-linear relationship exists between the increase in oxygen consumption and the decrease in acclimation temperature (2.5 mm.³ O₂/gm./hr. increase per degree centigrade drop in temperature from 26° to 16° C.; 5.0 mm.³ O₂/gm./hr. increase per degree centigrade drop in temperature from 16° to 10° C.).

Comparison of nymphs and adults. Comparison of the oxygen consumption of nymphal and adult cockroaches (Figs. 1 and 3) that have been acclimated to and measured at the same temperatures shows that adult cockroaches consume more oxygen per gram than equal weight nymphs. Although the adult curve representing the control animals (26° C.) is displaced above the curve for the control nymphs (26° C.), the slopes are essentially parallel. With acclimation to 16° and to 10° C. small and large nymphs respond in a like manner and these curves have approximately the same slopes as the 26° C. curve. On the contrary, small and large adults show a differential response to the temperatures of acclimation (with extrapolation, the curves in Fig. 3 would intersect to the right). Small adults are responding to the decreased temperatures of acclimation with a greater increase in their weight-specific oxygen consumption than are large adults. Small adults are therefore doing a better job of acclimating than large adults and all sizes of nymphs are doing a better job than all sizes of adults.

DISCUSSION

The object of this investigation was to see if the insect *Periplaneta americana* could acclimate its metabolic activity to temperature. However, we would first like

to discuss an additional observation. We have found that adult cockroaches are living at a faster metabolic pace than are nymphs of approximately the same weight (see Figs. 1 and 3). Batelli and Stern (1913) showed that at all temperatures from 20° to 40° C. fly imagines consume more oxygen per unit body weight than did larvae. Similarly, it was found by Ludwig (1931) that the weight-specific oxygen consumption of adult Japanese beetles, *Popillia japonica*, was greater than that of the larvae. Referring to the Holometabola, Wigglesworth (1950, p. 413) has stated that "metabolism at a given temperature is generally much higher in the adult than in the larva and higher in the larva than in the pupa." Wigglesworth attributes this difference to the increased activity metabolism of the adult. Many investigators will speak of the typical "U-shaped" respiratory curve during the metamorphosis of holometabolus insects (see Edwards, 1953, for references).

The available data for the Hemimetabola (the insects in which there is little or no change in shape during ontogeny) are much less than for the Holometabola. Edwards (1953) presents a curve showing the change in weight-specific oxygen consumption from egg deposition through early adulthood of the milkweed bug *Oncopeltus fasciatus*. Within a few days after the last molt, adults consume more oxygen per gram per hour than do last instar nymphs. If the oxygen consumption during molt is ignored, then the curve resembles a flattened "U-shape." In this study early adult and late nymphal *Periplaneta americana* show a similar relationship. With increasing size of the adult, the characteristic fall in weight-specific oxygen consumption is observed.

We do not know what makes possible the elevated metabolic activity of the early adult cockroaches; we have not observed a difference in locomotor activity that would account for it. Perhaps the elevation in rate is a consequence of the metamorphosis from nymph to adult. A similar suggestion was offered by Groebbels (1925) to account for the increase in metabolic rate found during metamorphosis of *Rana* tadpoles.

Contrary to the generalized statement of Edwards (1953) that insects do not compensate metabolically to temperature, both nymphs and adults of *Periplaneta americana* adapted to 10° C. consume more oxygen, per animal and per gram, than equal weight control animals adapted to 26° C. when measured at the same temperature.

Lühmann and Drees (1952) and Marzusch (1952) show temperature adaptation in four species of insects, two of which are overwintering (the potato beetle, *Leptinotarsa decemlineata*, and the leaf beetle, *Phytodecta rufipes*) and two in summer sleep (the potato beetle, *Melasma populi*, and the leaf beetle, *Galeruca tana-ceti*). These investigators are unable to show temperature adaptation during the active feeding period. Lühmann and Drees have suggested that the compensatory response is masked by the high metabolic activity associated with feeding. We believe that if such a response can be demonstrated at any given time, it does seem reasonable to expect this ability to be present at all times. This expectation is borne out by *Periplaneta americana*, which is active and feeds all year. Therefore, it is difficult to understand why this compensatory response appears only in these insects under conditions of winter and summer sleep. It would be well to note that one species of leaf beetle (*Chrysomela haemoptera*) shows no adaptation even though its metabolic level was depressed during the summer sleep (Lühmann and Drees, 1952).

Previously, cold- and warm-adapted groups have been compared at a given temperature or between temperatures by arbitrarily choosing a weight and determining the oxygen consumption for each group. It is also profitable to choose an arbitrary rate of oxygen consumption and determine the approximate weight of animal in each group for which this rate is obtained (Figs. 1 and 3). As a generalization, a large cold-adapted cockroach consumes about as much oxygen as a small warm-adapted one. For example, a 0.4-gram nymph ($26^{\circ}\text{C}.$), a 0.7-gram nymph ($16^{\circ}\text{C}.$) and a 0.9-gram nymph ($10^{\circ}\text{C}.$) when measured at $20^{\circ}\text{C}.$ consume equal amounts of oxygen per unit weight. Similarly, it is possible to determine the temperatures at which cold- and warm-adapted roaches consume the same amount of oxygen (Fig. 2). On this basis, cold-adapted animals consume at $15^{\circ}\text{C}.$ slightly more oxygen than warm-adapted animals consume at $20^{\circ}\text{C}.$

Sayle (1928) tested the effect of low temperature on carbon dioxide production of dragon fly nymphs (*Aeschna umbrosa*). She lowered the temperature from $22^{\circ}\text{C}.$ to $13^{\circ}\text{C}.$ (three days at $17^{\circ}\text{C}.$ and three days at $13^{\circ}\text{C}.$) and found that carbon dioxide production was about the same at the lower temperature as the initial production at $17^{\circ}\text{C}.$ after the first day. The major portion of acclimation of these nymphs was evident within forty-eight hours. It is not unreasonable to expect that the rate of acclimation in *Periplaneta americana* is equally as rapid since no further change was evident after six days. In addition, animals measured at $20^{\circ}\text{C}.$ after spending a number of hours at $30^{\circ}\text{C}.$ consume less oxygen than animals measured at $20^{\circ}\text{C}.$ directly from $26^{\circ}\text{C}.$ Such time courses as found in these animals compare favorably with that shown for other species (Behre, 1918; *Planaria dorotocephala*; Roberts, 1952, *Pachygrapsus crassipes*; Segal, 1955, *Acmaca limatula*).

Bullock (1955) has thoroughly reviewed the known cases of acclimation to temperature at the several levels of organization (molecular, cellular, tissue and organ system). He does cite several negative instances in which animals fail to show acclimation. However, the evidence from widely divergent groups, involving different physiological systems, suggests to us that compensatory responses to environmental stresses are inherent components of protoplasmic systems. Negative cases as cited by Bullock (1955) do not invalidate this idea. Such instances suggest to us that animals, in which no acclimation was found in the particular physiologic system studied, might show compensation to stress in another system or at a different level. Compensatory responses to temperature are most often described, but other environmental parameters (osmotic pressure, drugs, oxygen tension; see Prosser, 1955) equally as important may evoke such adaptation. If this phenomenon is a universal component of living systems and permits animals to assume degrees of environmental independence, it goes far to explain their survival and distribution. Within limits it accomplishes the same results as homiothermism accomplishes for the warm blooded animals.

SUMMARY

1. Oxygen consumption has been studied in cultures of nymphal and adult cockroaches, *Periplaneta americana*, that have been maintained at two experimental temperatures (10° and $16^{\circ}\text{C}.$) and the control temperature ($26^{\circ}\text{C}.$) for a period of one to three weeks.

2. It has been shown that the oxygen consumption of equal-weight nymphs when measured at 20° C. is higher in animals that have been maintained at the lower temperatures.

3. Comparison of cold- (10° C.) and warm-adapted (26° C.) nymphs when measured at a series of temperatures (10° to 25° C.) demonstrates that cold-acclimated animals consume more oxygen per gram per hour than equal weight warm-adapted ones.

4. Adult cockroaches show acclimation of their oxygen consumption to temperature. However, there is a differential response with respect to size; small adults acclimate to a greater degree than large ones. Further, all sizes of nymphs show a greater degree of acclimation than all sizes of adults.

LITERATURE CITED

- BATELLI, F., AND L. STERN, 1913. Intensität des respiratorischen Gaswechsels der Insekten. *Biochem. Zeitschr.*, **56**: 50-58.
- BEHRE, E. H., 1918. An experimental study of acclimation to temperature in *Planaria dorotocephala*. *Biol. Bull.*, **35**: 277-317.
- BULLOCK, T. H., 1955. Compensation for temperature in the metabolism and activity of poikilotherms. *Biol. Rev.*, **30**: 311-342.
- CLOUDSLEY-THOMPSON, J. L., 1953. Studies in diurnal rhythms. III. Photoperiodism in the cockroach *Periplaneta americana* (L.). *Ann. Mag. Nat. Hist.*, **6**: 705-712.
- DEHNEL, P. A., 1955. Rates of growth of gastropods as a function of latitude. *Physiol. Zool.*, **28**: 115-144.
- EDWARDS, G. A., 1953. Quoted in Chapter 5, *Insect Physiology*, edited by K. D. Roeder. J. Wiley and Sons, New York.
- GROEBBELS, F., 1925. Untersuchungen über Wachstum, Entwicklung und Stoffwechsel von Froschlarchen unter verschiedenen Bedingungen der Ernährung. *Arch. ges. Physiol.*, **208**: 718-729.
- HELLER, J., 1930. Sauerstoffverbrauch der Schmetterlingsspinnen in Abhängigkeit von der Temperatur. *Zeitschr. verg. Physiol.*, **11**: 448-460.
- LUDWIG, D. J., 1931. Studies on the metabolism of the Japanese beetle (*Popillia japonica* Newman). I. Weight and metabolism changes. *J. Exp. Zool.*, **60**: 309-323.
- LÜHMANN, M., AND O. DREES, 1952. Über die Temperaturabhängigkeit der Atmung sommerschlafender Blattkäfer. *Zool. Anz.*, **148**: 13-22.
- MARZUSCH, K., 1952. Untersuchungen über die Temperaturabhängigkeit von Lebensprozessen bei Insekten unter besonderer Berücksichtigung winterschlafender Kartoffelkäfer. *Zeitschr. verg. Physiol.*, **34**: 75-92.
- PARHON, M., 1909. Les échanges nutritifs chez les abeilles pendant les quatre saisons. *Ann. Sci. Nat. (ser. 9), Zool.*, **9**: 1-58.
- PARKER, J. R., 1930. Some effects of temperature and moisture upon *Melanoplus mexicanus mexicanus* Saussure and *Camilla pellucida* Scudder (Orthoptera). Univ. Montana, Agri. Exp. Sta., Bull. 223, 1-132.
- PROSSER, C. L., 1955. Physiological variation in animals. *Biol. Rev.*, **30**: 229-262.
- ROBERTS, J. L., 1952. Studies on acclimatization of respiration to temperature in the lined shore crab, *Pachygrapsus crassipes* Randall. Ph.D. dissertation, Univ. of California, Los Angeles.
- SAYLE, M. H., 1928. Factors influencing the rate of metabolism of *Aeschna umbrosa* nymphs. *Biol. Bull.*, **54**: 212-230.
- SCHOLANDER, P. F., W. FLAGG, V. WALTERS AND L. IRVING, 1953. Climatic adaptation in arctic and tropical poikilotherms. *Physiol. Zool.*, **26**: 67-92.
- SEGAL, E., 1955. Microgeographic variation as thermal acclimation in an intertidal gastropod. Ph.D. dissertation, Univ. of California, Los Angeles.
- THOMPSON, V., 1937. Effects of temperature on movements of embryos (Acrididae, Orthoptera). *Physiol. Zool.*, **10**: 21-30.
- WIGGLESWORTH, V. B., 1950. *Insect physiology*. E. P. Dutton and Co., Inc., New York.